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Plant-parasitic Nematodes in Iowa[1]

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Ninety-nine species of plant-parasitic nematodes are recorded from Iowa. Twenty-seven are new state records. Most samples were collected from around maize or from prairies or woodlands. Similarity (Sorensen's index) of species was highest for the maize-prairie habitats (0.49), compared with maize-woodlands (0.23), or prairie-woodland (0.37) habitats. Nematode communities were most diverse in prairies with a Shannon-Weiner index (H') of 2.74, compared with 1.65 and 1.07 for woodlands and maize habitats, respectively. Evenness of species (J') was 0.41, 0.78, and 0.48 for maize, prairies, and woodlands, respectively.
INDEX DESCRIPTORS: Nematodes, maize, prairies, woodlands, ecology

Although nematodes are the most numerous multicellular animals and include more species than any other Metazoa, except for the arthropods, they are known mainly to parasitologists and plant nematologists. The best known groups of nematodes probably are the animal parasites that usually are studied in parasitology and medicine. Study of the occurrence and distribution of nematodes parasitizing plants is more than academic. Many are important pathogens that reduce yields or aesthetic appeal and, in some instances, prohibit crop production. Plant-parasitic nematodes range from 300 µm to more than 8 mm long, but most are a millimeter or less. Of the species attacking plants, those in the genera *Heterodera*, *Meloidogyne*, and related forms are the best known because they are widespread and many are important pathogens. Much of the nonfamiliarity with the plant-parasitic forms is because they are generally microscopic, and most live underground. Nematodes have been collected in Iowa for nearly 30 years, with emphasis on agricultural crops. Most collections from nonagricultural soils have been made since 1983 as a result of a grant from the Iowa Science Foundation, but a few studies were made previously in prairies and woodlands (19,32,34,43,45). Results reported here include corrections of earlier Iowa records and nomenclatorial changes owing to taxonomic revisions. Annotations are made on morphologies and distributions in many instances.

MATERIALS AND METHODS

Samples were taken in the rhizosphere of the target plants. Maize (*Zea mays L.*) was the cultivated plant most frequently sampled. Samples from the rhizosphere of plant species were made in prairies and woodlands; attempts were made to keep roots of undesired species to a minimum. In woodlands, soil around rootlets emanating from the primary roots was selected. Care was taken to avoid collection where herbaceous plants were near the tree sampled.

A sample consisted of 200-500 cm^3 of soil and fibrous roots collected with a 2.5-cm-diameter core sampler, a shovel, or trowel as the situation dictated. Samples were usually taken to a depth of 15-30 cm and were returned to the laboratory. Soil (100 cm^3) from each sample was processed by centrifugal flotation (21), and nematodes were extracted from fibrous roots by the 4-day shaker method (4). Samples were refrigerated at 3 C until processing which was usually within 2-3 days after sampling. Counts given are for 100 cm^3 of soil or per gram of dry root. Count figures are for nematodes in the soil unless specified for roots. Where root-knot nematodes were suspected, females, if present, were dissected from the roots. Cultivated plants, especially maize were collected statewide. The major natural areas from which samples were collected are listed in Table 1. Quantitative data for diversity and similarities indices are based on 404, 119, 358 samples collected since 1984 from maize, prairies, and woodlands, respectively. Diversity (H') and evenness (J') were measured by the equations $H' = -\Sigma pi \log pi$ and $J' = H'/H'max$, respectively (38). Similarity indices were those of Sorensen (51). Representative specimens were mounted on Cobb slides and deposited in the Iowa State University plant-nematode collection in the Department of Plant Pathology. Many individuals were not identified for various reasons, which include poor preservation, immature specimens, insufficient material, and seemingly undescribed species.

Two contrasting treatments of the Tylenchida have been published recently; one by Siddiqi (48) and, the other, in a series of articles in the Revue de Nématologie (11,12,13,25,26,27,28,29,39,40). I have followed the latter treatments here.

Table 1. Numbers of soil samples collected for plant-parasitic nematodes in natural areas. Iowa, 1984-1987.

County	Location	Number of samples
Allamakee	Yellow River Forest	20
Black Hawk	Cedar Hills Sand Prairie	16
Boone	Iowa Arboretum	11
Boone	Ledges State Park	5
Butler	Heery Woods State Park	5
Clayton	Pikes Peak State Park	10
Delaware	Backbone State Park	10
Dubuque	White Pine Hollow Preserve	30
Fayette	Brush Creek Canyon Preserve	30
Fayette	Volga River State Forest	15
Floyd	Idlewild County Park	2
Fremont	Waubonsie State Park	5
Hancock	Pilot Knob State Park	8
Hardin	Pine Lake State Park	4
Hardin	Tower Rock County Park	10
Lee	Donnellson Unit, Shimek State Forest	11
Lucas	Lucas Unit, Stephens State Forest	10
Lyon	Gitchie Manitou	10
Monona	Lewis and Clark State Park	10
Monona	Loess Hills north of Turin	24
Monona	Preparation Canyon State Park	16
Muscatine	Wild Cat Den State Park	19
Van Buren	Lacy-Keosauqua State Park	10
Webster	Brushy Creek Recreational Area	1
Webster	Dolliver Memorial State Park	20
Webster	Woodman Hollow Preserve	20
Woodbury	Liberty Wildlife Area	8
Woodbury	Stone State Park	15

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RESULTS AND DISCUSSION

Ninety-nine species of plant-parasitic nematodes are recorded from Iowa, of which 27 are new state records. Although many species are economically important, most species included here have not been sufficiently investigated to measure their economic importance. The most plant-parasitic species found in one sample was nine around *Ulmus americana* L. at Brush Creek Canyon. The number of species per plant averaged 2.9, 3.6, and 4.9 for maize, woodlands, and prairies, respectively.

ANGUINIDAE Nicoll, 1935

Ditylenchus Filip'ev, 1936. Three collections from roots of maize contained species of this genus; in one over 2,000 individuals were recovered. This genus is not well investigated in Iowa.

Subanguina Paramonov, 1967. The only species found in Iowa causes galls on leaves of *Calamagrostis* spp.

S. calamagrostis (Wu, 1967) Brzeski, 1981. This species is a common parasite of *Calamagrostis canadensis* (Michx.) Beauv. and *C. inexpansa* A. Gray in wet native prairies. The nematode has been found in the Bergman, Crossman, Hayden, Mark Sand, Steele, Stinson, and Williams prairies, as well as in *C. canadensis* in Ohio and Wisconsin (36) and in Canada (61). The nematode probably occurs in Minnesota, but this needs to be confirmed (36).

DOLICHODORIDAE Chitwood, 1950.

Dolichodorus Cobb, 1914

D. heterocephalus Cobb, 1914. This was associated with grass by the Skunk River, Inis Grove Park, Ames.

BELONOLAIMIDAE Whitehead, 1960

Belonolaimus Steiner, 1949.

B. nortoni Rau, 1963. Kerr and Wysong (22) stated that a *Belonolaimus* sp. associated with maize in Nebraska was close to *B. nortoni* except that the "... female tail and spear lengths are slightly larger and the vulva lips less protruding than originally described for *B. nortoni*. Males differ by having a slightly longer tail." Specimens that I collected around grass near Sergeant Bluff in Woodbury County and from maize in Holt and Rock counties, Nebraska and in natural range in Rock County generally agree with the conclusions stated by Kerr and Wysong. Most stylet and tail lengths that I examined were in the upper range given by Rau (41). Rau reported that *B. nortoni* has protruding vulval lips. The vulval lips in my material ranged from not protruding to slightly protruding in the same population. In Iowa, the nematode was collected around grass in a sandpit near the Liberty Wildlife area at Sergeant Bluff, Woodbury County, around maize in Pottawattamie County, and around silver maple (*Acer saccharinum* L.) in Inis Grove Park, Ames.

Geocenamus Thorne & Malek, 1968

G. longus (Wu, 1969) Tarjan, 1973. This species was associated only with balsam fir [*Abies balsamea* (L.) Mill.] at the Bluffton fir stand. The only other recorded occurrences in North America are from soil around *Populus balsamifera* L. Bow River Forest, Calgary, Alberta, Canada (62) and soil around *Betula* sp., Douglas Lake, Michigan (23). In Europe, the nematode is widely distributed in forest in West Germany. In Poland, the nematode has been found in several localities associated with *Betula verrucosa* (7,52). The nematode is possibly holarctic.

G. tenuidens Thorne and Malek, 1968. This species was found associated only with *Yucca glauca* Nutt. in Stone Park. Elsewhere in the United States it has been found in prairie sod near Rugby, North Dakota (56), from South Dakota and prairie sod in Manitoba, and in alpine meadows in California (52). All areas were glaciated either by continental or alpine glaciers. In Germany, the nematode has been found only in grasslands in the northern half of the country. It has also been associated with strawberries (*Fragaria* sp.) in Poland (53). Thus, it is a rare nematode seemingly with a narrow ecological amplitude.

TELOTYLENCHINAE Siddiqi, 1960

Merlinius Siddiqi, 1970

Merlinius joctus (Thorne, 1949) Sher, 1974 was found at the Cayler and Kalsow prairies (43) and around perennials in a home garden.

Nagelus Thorne & Malek, 1968

N. leptus (Allen, 1955) Siddiqi, 1979 was found mainly in woods, but it was also found in lawn turf. The highest count in woods was 250 around Kentucky coffee tree [*Gymnocladus dioica* (L.) K. Koch] at the Iowa Arboretum.

Tylenchorhynchus Cobb, 1913. The species reported here are commonly associated with naturally occurring and cultivated grasses.

T. acutoides Thorne and Malek, 1968. This was collected around *Petalostemon purprueum* (Vent.) Rydb. at the Freda Haffner Kettlehole in Dickinson County. It is also known from native sod in Montana, North Dakota, and South Dakota (56).

T. acutus Allen, 1955. This is a common nematode around maize and other grasses, especially in well-drained loess soils. The maximum numbers obtained, 650-700, were around maize in Woodbury County. It is also common in the Fred Haffner Kettlehole and prairies of the loess hills.

T. agri Ferris, 1963 is occasionally associated with maize. The greatest population was 210 in Black Hawk County. It also was found at the Freda Haffner Kettlehole, with a high count of 270, and in the isolated prairie patches at Woodman Hollow.

T. annulatus (Cassidy, 1930) Golden, 1971 was uncommon, but was found occasionally in prairies and maize. However, a count of 2,470 occurred in the hanging peat bog in Plymouth County, the only high count obtained.

T. capitatus Allen, 1955. A count of 80 was found in the soil around *Yucca glauca* in the loess hills at Waubonsie State Park. The length was 85 μm, which is in the upper range of measurements given by Allen (1). The excretory pore was at the middle instead of at the beginning of the esophageal bulb as given by Allen.

T. claytoni Steiner, 1937 was associated with stunted maize in highly sandy soils in Black Hawk, Butler, and Muscatine counties. The nematode was also collected at the Cedar Hills Sand Prairie where it is probably native. The highest count was 280, with a mean of 100 in the six samples in which the species was identified.

T. emericolus Allen, 1955 was found in one sample each in the Kalsow and Cedar Hills Sand prairies. The highest count was 90.

T. maximus Allen, 1955 is common in lowland prairies and in turf. It was not found in the dry prairies of the loess hills or the hill-prairies around Dubuque. The highest count obtained was 2,360 in a pasture in Worth County. The highest count in any native prairie was 552 at the Kalsow Prairie. A nematode that fits *T. maximus* in most respects was found around grasses in the loess hills north of Turin. The main difference in this nematode from *T. maximus* is that this nematode has males. Otherwise the females have similar measurements and appearance to *T. maximus*.

T. nudus Allen, 1955. One of the most common parasitic nematodes associated with maize in all but the loess soils of western Iowa. The mean number associated with maize was 38, with a maximum of 266 in Allamakee County. It is also common in the Cayler, Kalsow, and Sheeder prairies.

T. silvaticus Ferris, 1963. Although the species was found in Shimek State Forest, this nematode is basically a prairie species being found in the grasslands of the Cayler, Kalsow, and Sheeder prairies and in grasslands at Gitchie Manitou and the Mines of Spain. The maximum count was 520 with a mean of 70 for the 17 samples in which it was found.

PRATYLENCHIDAE, Thorne, 1949

Hirschmanniella Luc & Goodey, 1964

H. gracilis (de Man, 1880) Luc & Goodey, 1964 is a nematode of wet places. It was found around cattail (*Typha* sp.) in Little Wall Lake (59), Lewis and Clark State Park, and sedge (*Cyprus* sp.) in the Cedar Hills Sand Prairie.

Pratylenchoides Winslow, 1958

P. heathi Baldwin, Luc & Bell, 1983. This species was associated with basswood (*Tilia americana* L.) in the Paint Creek Area at Yellow River. Williams (59) reported *P. erzurumensis* as being associated with *Ambrosia trifida* L. in Story County. On further examination of the material, these nematodes have been identified as *P. heathi*.

Pratylenchus Filip'ev, 1936. Lesion nematodes. Because of their widespread distribution and proven pathogenicity, species of this genus are among the most common and economically important nematodes attacking maize and soybeans [*Glycines max* (L.) Merr.] in Iowa. They are found occasionally in woodlands and native prairies, but cultivated agriculture has favored their existence. They are basically endoparasitic. It is common for more than one species to occur in a sample, making counts per species subject to considerable error. Some species are difficult to identify. Frequently species identifications were not made in routine surveys and much extension work, total counts in the genus serving as the record. Numbers per gram of dry root sometimes could be greater than 50,000. From 385 maize samples, the mean number per gram of dry root was 3,400, with a maximum of more than 84,000. From 40 soybean samples, the mean was 2,846 with a maximum of 31,000. From 299 woodland samples, species of *Pratylenchus* were found only four times. The nematodes were found in only nine of 118 prairie samples. Quantitative data for the combined *Pratylenchus* species associated with maize were given by Norton (31).

P. alleni Ferris, 1961. This is the third most common species of the genus associated with maize. Although it is statewide and is found in many different soil types, it has been recovered most frequently from roots of maize growing in loess soils in the western third of Iowa and in sandy soils elsewhere. The most found was 27,000 per gram of dry root from maize in Woodbury County. The nematode was found in small numbers at the Williams Prairie.

P. convallariae Seinhorst, 1959. The only material available is from maize in Monona County. The morphometrics agree with the original description except that the tail annules are more coarse than described by Seinhorst (46), being more like that illustrated by Loof (24). The tail is somewhat more truncate, as illustrated by Loof.

P. flakkensis Seinhorst, 1968. An uncommon species found occasionally around maize and other grasses. The tails are more coarsely annulated than described by Seinhorst (47). Besides the reports of Thomas and Norton (54) and Williams (59), the nematode was found around maize in Monona, Ringgold, and Winnebago counties, alfalfa (*Medicago sativa* L.), and grass in Wapello County; and from grasses at the Retz Memorial and Gitchie Manitou preserves. The highest count in maize roots was 1,100 (59).

P. hexincisus Taylor & Jenkins, 1957. Possibly this is the most common species of the genus in the state, at least in maize. It has also been found around *Yucca glauca* in the loess hills near Turin and around little bluestem [*Schizachyrium scoparium* (Michx.) Nash] in the hill-prairies near Dubuque.

P. neglectus (Rensch, 1924) Filip'ev & Schuurmanns Stekhoven, 1941. Williams (59) found this species associated with maize in Benton and Lee counties, with counts in the roots being 4,000 or less. Had we made more species identification, the nematode probably would be more extensively known in Iowa than our records indicate.

P. scribneri Steiner, 1943. Along with *P. hexincisus*, *P. scribneri* is one of the most common nematodes of the genus in maize. It is statewide and found in a variety of soils, although I have the impression that *P. hexincisus* is more common in the heavier soils. In native areas few *P. scribneri* were found.

P. thornei Sher & Allen, 1953. Although several records from maize were listed as *P. thornei*, I have no voucher specimens. A voucher is available from strawberries in a nursery in southwestern Iowa, where the nematode was possibly shipped in.

P. vulnus Allen & Jensen, 1951. Schmitt (44) reported this nematode in lilac from a nursery in southwestern Iowa, where it was possibly introduced.

HOPLOLAIMIDAE Filip'ev, 1934. This family contains some of the most common plant parasites in Iowa. Agricultural practices certainly favor some species, but many species doubtless have been eliminated under cultivation.

Aorolaimus Sher, 1963

A. baldus Thorne & Malek, 1968 is a common nematode in the loess hill prairies along the western edge of Iowa. It was recovered from Waubonsie and Preparation Canyon state parks, the loess hills north of Turin to the loess hills in Stone Park north of Sioux City. It was never found in wooded areas. The nematode was obtained in 21 samples, with an average of 134 and a maximum of 790. The only previous reports are from South Dakota (49,50,56). I also collected it around lead plant (*Amorpha canescens* Pursh) and grass in the Willa Cather Prairie near Red Cloud, Nebraska.

A. torpidus Thorne & Malek, 1968. This species was found in the Hayden Prairie and around boxelder (*Acer negundo* L.) with grass cover at the Ames High Prairie. Thorne and Malek (56) recorded the stylet as 23 μm long. Examination of material marked "1 *Aorolaimus torpidus*" from South Dakota, and kindly supplied by James D. Smolik, revealed the stylet to be about 32 μm. I suspect that the original was a reverse typographical error.

Helicotylenchus Steiner, 1945.

Many samples contained individuals of *Helicotylenchus* that were not identified.

H. anhelicus Sher, 1966. This species was associated with *Acer negundo* in Lee County and with canary grass (*Phalaris canariensis*) L. in Story County, both along the Skunk River. The maximum number was 344. I also collected this species around sandbar willow (*Salix interior* Rowlee) in sandy soil near the Platte River just south of Grand Island, Nebraska.

H. californicus Sher, 1966. It was associated with *Calamagrostis canadensis* in the Williams Prairie, *Carex* sp. in the Cedar Hills Sand Prairie, and *Sagittaria latifolia* Willd. in the Freda Haffner Kettlehole, where the largest population of 1,930 occurred.

H. digonicus Perry in Perry, Darling & Thorne, 1959. This species was common in all prairies examined with the largest population being 2,120 in the hill-prairies near Dubuque. I also collected it at the Willa Cather Prairie near Red Cloud, Nebraska.

H. dihystera (Cobb, 1893) Sher, 1961 is a common nematode in prairies, often in the drier sites. It was found at the Ames High School, Gitchie Manitou, Kalsow, Freda Haffner Kettlehole, Cedar Hills Sand and Williams prairies, the loess hills north of Turin, Preparation Canyon, and Stone Park, and the small prairie bluffs at Woodman Hollow. Common associates were big (*Andropogon gerardi* Vitman.) and little bluestems, side oats grama [*Bouteloua curtipendula* (Michx.) Torr.], and Indiangrass (*Sorghastrum nutans* L.) Nash. The maximum number, 740, was around lespedeza (*Lespedeza capitata* Michx.) and grass at Gitchie Manitou. Pathotypes also exist because the nematode is common around maize in the southern United States, but I have never found it associated with maize in Iowa. I have found it commonly associated with maize in Colombia, South America (35). The species is variable morphologically (15). A few were associated with shagbark hickory [*Carya ovata* (Mill.) K. Koch] at the Dolliver Memorial.

H. exallus Sher, 1966. This uncommon species was associated with *Verbena stricta* Vent. at the Freda Haffner Kettlehole, *Carya ovata* at the Childs Access in Black Hawk County, various prairie plants in the Kalsow Prairie (43),and turf in Shelby County, which contained the largest population found of 403. The mean in all samples in which the nematode was found was 155.

H. hydrophilus Sher, 1966. Schmitt (43) found this in potholes at the Kalsow Prairie.

H. labiodiscinus Sher, 1966 was found only in the drier prairie sites at Ames High School, Gitchie Manitou, Hayden, Dubuque, Cedar Hills Sand and Sheeder prairies, and at the loess hills near Turin. The largest population of 1,470 was found around big bluestem north of Turin.

H. leiocephalus Sher, 1966 was found at the Cayler, Kalsow, and Williams prairies.

H. platyurus Perry in Perry, Darling & Thorne, 1959 is common in woodlands in all parts of the state, but has been found in small patches of prairies adjoining woodlands. It was found in 55% of all woodland samples and occurred in 68% of 19 *Carya ovata* samples, and 62% of 37 ironwood [*Ostrya virginiana* (Mill.) K. Koch] samples. The largest population of 850 occurred around black cherry (*Prunus serotina* Ehrh.) at Pilot Knob State Park. Few were found around conifers.

H. pseudorobustus (Steiner, 1914) Golden, 1956. This is one of the most common plant-parasitic nematodes in Iowa. Although the nematode occurs in woodlands and native prairies, agricultural practices has favored this species. It probably can be found in every established maize or soybean field because both plants are good hosts. The largest number, 2,570, was found in March in overwintered maize in Des Moines County. Generally, few were found in highly sandy soils (31). The record also include specimens of *H. bradys* Thorne & Malek, 1968, which Boag and Jairajpuri (5) maintained as a separate species, but which was made a synonym of *H. pseudorobustus* by Fortuner et al. (14).

Hoplolaimus von Daday, 1905.

H. galeatus (Cobb, 1913) Thorne, 1935. This was the only species of the genus found in Iowa. It was obtained from 12, 14, and 1% of the roots processed for endoparasites of maize, prairies, and woodlands, respectively. The maximum found was 2,597, 419, and 113/g dry root from maize, prairie plants, or woodland plants, respectively. Numbers were usually few, but when numbers were greater than 1,000/g dry root, plants were severely stunted. Most large numbers were from maize plants in sandy soils in the southeastern part of the state.

Pararotylenchus Baldwin & Bell, 1981.

P. blothrotylus Baldwin & Bell, 1981. This species was found only around *Abies balsamea* and yew (*Taxus canadensis* Marsh.) at the Postville fir stand and around sugar maple (*Acer saccharum* Marsh.) in Brush Creek Canyon. The maximum count was 430 around *A. balsamea*. The only other North American report is around wild rose (*Rosa* sp.) in Soldier Canyon, Sevier County, Utah (3).

P. hopperi Baldwin & Bell, 1984. This species was found only around herbs and white pine (*Pinus strobus* L.) at the Bluffton fir stand and White Pine Hollow where the maximum number found was 208. Elsewhere in North America, it was associated with quaking aspen (*Populus tremuloides* Michx.) at 7,500 feet in the Wasatch National Forest, Utah (20).

Rotylenchus Filip'ev, 1936.

R. pumilus (Perry *in* Perry, Darling & Thorne, 1959) Sher, 1961. Associated with mulberry (*Morus* sp.) in Pammel Woods, Ames, Iowa.

HETERODERIDAE Filip'ev & Schuurmans Stekhoven, 1941

HETERODERINAE Filip'ev & Schuurmans Stekhoven, 1941

No major attempt has been made to make an extensive survey for these nematodes except in two instances. These are among our most damaging forms. Cysts are common in soil and have been found in diverse habitats; doubtless many more species than those treated below occur in Iowa.

Cactodera Krall' & Krall', 1978

C. betulae (Hirschmann & Riggs, 1969) Krall' & Krall', 1978. Species of birch (*Betula*) are the best known hosts, although the nematode can reproduce in other woody plants (42). The only known occurrence of the nematode in Iowa is that of Golden and Raski (16) who reported that it occurred near Mason City, host not specified.

C. weissi (Steiner, 1949) Krall & Krall, 1978. A common species parasitizing smartweed (*Polygnum* spp.). The nematode is generally found wherever the weed occurs.

Heterodera Schmidt, 1871

H. glyncines Ichinohe, 1952. This is known as the soybean cyst nematode. It perhaps is the best known plant-parasitic nematode in the state because of its pathogenicity to soybeans. It was found in Winnebago County in 1978 and in 1988 was known in 35 counties but it doubtless occurs in many more.

H. trifolii Goffart, 1932. This is known as the clover cyst nematode, and it probably is the most widespread of any cyst nematode in Iowa. It can be pathogenic and is likely to be found wherever white (*Trifolium repens* L.) or red (*T. pratense* L.) clovers occur, such as in lawns and pastures.

Meloidodera Chitwood, Hannon & Esser, 1956. A species of this genus has been found in Iowa and Nebraska parasitizing maize in highly sandy soils. It has sometimes been given the epithet of *M. charis* Hopper, 1960, but the material that I examined from both states is much smaller than that species. A taxonomic study is needed.

MELOIDOGYNINAE Skarbilovich, 1959

Meloidogyne Goeldi, 1892. Species in this genus are among the most damaging and widespread plant-parasitic nematodes in the world. The symptoms are well known and are usually called to the nematologists' or plant pathologists' attention when cases are severe. Only two species have been identified as occurring in Iowa, although collections have been made from prairies that seem to fit other species, but positive identifications have not been made.

M. hapla Chitwood, 1949 is called the northern root-knot nematode. This species frequently occurs in home gardens, commercial vegetable plantings, ornamentals, and alfalfa. Dandelion (*Taraxacum officinale* Weber) is also a host and doubtless maintains the pest in pastures and other places. Two factors keep this nematode from being an important pest in Iowa. Maize is immune to this nematode and keeps the pest under control where maize is rotated with other crops. Also, damage is most noticeable in sandy soils, which generally occur locally in Iowa. Damage can occur in light textured soils, but the loss is usually attributed to winter injury or other factors.

M. ovalis Riffle, 1963. This probably is the most common root-knot nematode in the state. It is not well known because it occurs in woodlands where it attacks black walnut (*Juglans nigra* L.), maple (*Acer* spp.), ash (*Fraxinus* spp.), and many other trees.

CRICONEMATIDAE Taylor, 1936. Species of this family are common in natural areas and are found only occasionally in Iowa where land is cultivated.

CRICONEMATINAE Taylor, 1936.

Criconema Hofmanner & Menzel, 1914

C. lamellatum (Raski & Golden, 1966) Raski & Luc, 1984. This species is scattered in woodlands throughout the state. Hoffmann (18) found it in Pammel Woods at Iowa State University and Red Hawk State Park. Other known occurrences are at Dolliver, Pikes Peak, Ledges, the Iowa Arboretum, Maquoketa, Woodman Hollow, and Yellow River. The species was found 21 times, with maximum counts of 150 around *Juglans nigra* at Pikes Peak State Park and *Gymnocladus dioica* at the Iowa Arboretum. The mean number of all samples was 42.

C. permistum (Raski & Golden, 1966) Raski & Luc, 1984) was found 22 times, nearly all in sand prairies. The mean number was 64 with a maximum count of 330 around *Calamagrostis canadensis* at the Cedar Hills Sand Prairie.

C. petasum (Wu, 1965) Raski & Luc, 1984. This is a widely distributed, but infrequently found species. We recovered it only 20 times, all in woodlands: Backbone, Brush Creek Canyon, Dolliver, Ledges, Maquoketa, Pine Lake, Pikes Peak, White Pine Hollow, Wild Cat Den, Yellow River, and Volga River state parks or preserves. The most was 270 around *Pinus strobus* at Pine Lake State Park.

C. sphagni Micoletzky, 1925 was found only around yellow birch (*Betula lutea* Michx.) at Tower Rock. This species is common around trees growing in acid soils of the northeastern states of the U.S.A. (19). The Iowa collections and some from northern Minnesota (18) are the farthest west known occurrences of this species.

Criconemella De Grisse & Loof, 1965

Criconemella sp. #1. This evidently is a new species. It was found only in the dry loess bluffs in the Loess Hills from Preparation Canyon to Stone Park in western Iowa. The highest count was 120, with a mean of 48 in the eight samples in which the nematode was identified. Specimens are deposited in the U.S.D.A. nematode collection at Beltsville, Maryland.

C. axestis (Fassuliotis & Williamson, 1959) Luc & Raski, 1981. Hoffmann (18) reported it to be associated with *Carya ovata* in the Donnelson Unit of Shimek State Forest and around *Tilia americana* in the Yellow River Forest Preserve.

C. bakeri (Wu, 1965) Luc & Raski, 1981 was found only around *Abies balsamea* and *Pinus strobus* at the Bluffton fir stand. The juveniles have beaded or very short fringed annules, and thus would not fit in with the limits set by Raski and Luc (40), who state that the juvenile annules are smooth to crenate with three exceptions. Whether *C. bakeri* is another exception remains to be seen. Wu (60) did not mention juveniles in her description of the nematode. Certain related species have been confusing to taxonomists, but for now, the nematode is given the epithet of *C. bakeri*. Specimens have been deposited in the U.S.D.A. nematode collection, Beltsville, Maryland.

C. curvata (Raski, 1952) Luc & Raski, 1981 was found in only five samples with the highest count being 360 in turf in Muscatine County. It was also found around maize in Black Hawk County, and at the Cedar Hills Sand Prairie, and at Melanphy Springs in Winneshiek County.

C. discus (Thorne & Malek, 1968) Luc & Raski, 1981. Hoffmann (18) reported this as occurring in the Kalsow Prairie. I found it associated with sedge and grass in Louisa County.

C. incrassata (Raski & Golden, 1966) Luc & Raski, 1981 was found 39 times, all in woodlands. The mean count was 41, with a high of 300 around *Prunus serotina* in Wild Cat Den State Park.

C. informis (Micoletzky, 1922) Luc & Raski, 1981. Hoffmann (18) collected this nematode around sweet corn in a home garden in Ames.

C. inusitata (Hoffmann, 1974) Luc & Raski, 1981. This species was collected in Pammel Woods at Iowa State University (17) and around wild rye (*Elymus virginicus* L.) along the Kate Shelly Trail in Boone County.

C. macrodora (Taylor, 1936) Luc & Raski, 1981. One of the most common nematodes in woodlands, it was found in 31% of the samples. The only time that it was found outside woodlands was in a maize field adjacent to woods. In woodlands, the nematode was found 116 times, with a mean count of 216 per sample and a maximum of 3,000 around *Ostrya virginiana* at Woodman Hollow. It was found in 71% of 17 bur oak (*Quercus macrocarpa* Michx.) samples and 61% of 18 white oak (*Q. alba* L.) samples, tree species of mainly upland habitats in Iowa.

C. pseudosolivaga (De Grisse, 1964) Luc & Raski, 1981 was found at the Williams and Cayler prairies and those at the Kettlehole and Mines of Spain. The mean of five samples was 165, with a high of 570 associated with *Solidago* sp. at the Mines of Spain.

C. raskiensis (De Grisse, 1964) Luc & Raski, 1981 was found in only five samples in nonwoodland habitats at the Cedar Hills Mark Sand Prairie, the Freda Haffner Kettlehole, Stone Park, and in Boone County. The maximum was 560 around *Scirpus* sp. in the Kettlehole. In the U.S.A., the species was found beneath grass in North Dakota (9) and on a slough bank in South Dakota (56).

C. reedi (Diab & Jenkins, 1966) Luc & Raski, 1981 was collected by Hoffmann (18) around *Typha angustifolia* L. at the Donnelson Unit of Shimek State Forest. I also collected it around river birch (*Betula nigra* L.) and weeds in the same area.

C. rustica (Micoletzky, 1915) Luc & Raski, 1981. Counts were made from 15 samples, mostly around grasses at the Williams Prairie and the Mines of Spain, but also from a few varied habitats and plants. The highest count of 280 was in the Williams Prairie.

C. sphaerocephala (Taylor, 1936) Luc & Raski, 1981 is known from only six samples at five locations, all around grasses. The most found were 190 around *Schizachyrium scoparium* on the loess bluffs at Stone Park.

C. xenoplax (Raski, 1952) Luc & Raski, 1981. Two forms of the nematode are used here. Typical *C. xenoplax* is common in woodlands, but was generally found in less than 50% of the samples from any tree species. A short stylet form as described by Hoffmann (18) occurs infrequently in prairies and around maize growing in sandy soils.

Hemicriconemoides Chitwood & Birchfield, 1957

H. nitida Pinochet & Raski, 1975 is an uncommon species found only in woodlands, including those at Heery Woods, the loess hills, Preparation Canyon, Waubonsie, White Pine Hollow, and Yellow River. Numbers were generally fewer than 25 per sample.

Discocriconemella De Grisse & Loof, 1965

D. inarata Hoffmann, 1974 is an uncommon nematode found mainly around grasses, including those at the Kalsow and Sheeder prairies (17). I also found it associated with dogwood (*Cornus stolonifera* Michx.) and grass along the Kate Shelley Trail in Boone County.

Ogma Southern, 1914

O. cobbi (Micoletzky, 1925) Siddiqi, 1986 was collected only around *Carya ovata* at the Childs Access in Black Hawk County.

O. decalineatum (Chitwood, 1957) Andrassy, 1979 was found only five times, mainly in prairies. Except for a count of 4,300 around *Yucca glauca* in Stone Park, numbers were less than 200.

O. fimbriatum (Cobb *in* Taylor, 1939) Raski & Luc, 1987 was found only in woodlands in 13 samples, the most being 90 around *Pinus strobus* in White Pine Hollow. It was also found at the Retz Memorial, Shimek State Forest, and Ledges, Maquoketa, and Wild Cat Den state parks.

O. hungarium (Andrassy, 1962) Siddiqi, 1986 is a rare nematode in Iowa. Hoffman (18) recorded it from Shimek and Stephens state forests and at Pilot Knob and Wapello state parks. We also found it at Brushy Creek Recreational Area in Webster County and around *Populus tremeloides* in Black Hawk County. Few were found at any location.

O. menzeli (Stefanski, 1924) Sch. Stekhoven & Teunissen, 1938 is common in woodlands throughout the state, with an average of 58 nematodes in the 82 samples in which it was found. The most recovered was more than 850 around hackberry *Celtis occidentalis* L.) at Brush Creek Canyon.

O. octangulare (Cobb, 1914) Sch. Stekhoven & Teunissen, 1938 is cosmopolitan in woodlands, the only habitat in which the nematode was found. The average number was 140 in the 104 samples in which it was found, with a maximum of 860 around *Acer saccharum* at Yellow River Forest Preserve.

HEMICYCLIOPHORINAE Skarbilovich, 1959

Hemicycliophora de Man, 1921.

These nematodes with wide distinct annules, a long stylet, and the presence of an extra cuticle are mainly woodland species. Numbers found generally are less than 100, although there are exceptions.

H. ferrisae Brzeski, 1974 was associated with woody plants in woodlands mainly in the northeastern part of the state at the Retz Memorial and with *Acer saccharum* at the Bluffton fir stand. It was also found around bloodroot (*Sanguinaria canadensis* L.) at Oakland Mills State Park and white ash (*Fraxinus americana* L.) along the Kate

Shelley Trail in Boone County. This last sample contained high count of 200 for this species.

H. gracilis Thorne, 1955 was found only once, which was around *Ostrya virginiana* in the Donnelson unit of Shimek State Forest. Only 10 were recovered.

H. minora Wu, 1966. This species is widespread and was found 23 times with a mean count of 55 in the samples in which it occurred. It was found around woody plants at the Bluffton and Postville fir stands and around maples, oaks, or ironwood at Oakland Mills and Waubonsie state parks, the Retz Memorial in Clayton County, and in Story County, among other places. It was found mainly on upland sites. Brzeski (6) examined specimens associated with *Acer saccharum* at Oakland Mills State Park in Henry County.

H. nortoni Brzeski, 1974 was associated with grasses, goldenrod (*Solidago* sp.) and sunflower (*Helianthus* sp.) in the Williams Prairie, and by *Salix interior* along the Skunk River at Inis Grove Park in Ames, Story County (6).

H. similis Thorne, 1955 was found around *Phalaris canariensis* at Inis Grove Park in Ames, Story County.

H. uniformis Thorne, 1955 averaged 105 nematodes per 16 samples. It was associated with white birch (*Betula papyrifera* Marsh.) at the Bluffton fir stand, with plants in the Cedar Hills Sand Prairie, and around several trees in Backbone, White Pine Hollow, Woodman Hollow, Brush Creek Canyon, Wildcat Den, and Maquoketa state parks or preserves.

H. vaccinii Reed & Jenkins, 1963 was found around *Acer saccharinum* at Dolliver Memorial, and *Calamagrostis canadensis* at the Cedar Hills Sand Prairie.

H. vidua Raski, 1958 was found 18 times, with a mean of 64 nematodes per sample. This species was associated with many different plants, mostly trees in different habitats, including *Carya ovata* at the Childs Access in Black Hawk County, and with *Phalaris arundinacea* L. at the Retz Memorial.

TYLENCHULIDAE Skarbilovich, 1947

Gracilacus Raski, 1972 and *Paratylenchus* Micoletzky, 1922.

These genera contain some of the smallest plant-parasitic nematodes known. Many often pass through the finer sieves used in processing; thus, quantitative data are unreliable. Large numbers, however, are recovered in some instances. In addition, the preadult juveniles are frequently more resistant to desiccation than adults and the latter may be scarce under dry conditions.

G. acicula (Brown, 1959) Raski, 1962 was found in the Kalsow Prairie by Schmitt (43), and I recovered it around grass on the bluffs in Stone Park.

G. straeleni (De Coninck, 1931) Raski, 1976. This species was identified from 58 samples, with all but two of them being associated with woody plants. The two highest counts of 730 and 600 were associated with *Acer saccharum* in Maquoketa State Park and red oak (*Quercus rubra* L.) in Brush Creek Canyon, respectively. Many samples in woodlands contained a few nematodes of this genus but were not identified.

P. elachistus Steiner, 1949 was found around *Morus* sp. in Pammel Woods, Iowa State University.

P. microdorus Andrassy, 1959 was found at the Ames High School and the Kalsow (43) prairies, and is common around maize in the loess soils of western Iowa (33). It was also found in the dry hill-prairies and the Mines of Spain near Dubuque.

P. nanus Cobb, 1923. This was associated with *Agrostis* sp. turf in Hamilton County and with *Andropogon* sp. in the Hayden Prairie.

P. projectus Jenkins, 1956 was reported by Schmitt (43) from the Kalsow Prairie. It has also been associated with maize and other plants around the state.

P. tenuicaudatus Wu, 1961 was found around *Prunus* sp. at Pikes Peak State Park and around *Phalaris arundinacea* at the Retz Memorial.

APHELENCHOIDIDAE (Skarb., 1967) Paramonov, 1953

Aphelenchoides ritzema-bosi (Schwartz, 1911) Steiner, 1932. This is one of the bud and leaf nematodes and has been found occasionally from all areas of the state. It is best known in Iowa attacking the leaves of *Chrysanthemum* L. In Ames, it has been collected from leaves of chrysanthemum outside the president's home at Iowa State University and at the Iowa State University Horticulture Farm. The nematode probably is much more widespread than known, but foliar collections of known host species were few.

Bursaphelenchus xylophilus (Steiner & Buhrer, 1934) Nickle, 1970 is the pinewood or pine wilt nematode. This species has been found killing pines in 17 counties in the state. It was first found in Iowa in Shimek State Forest and since has been found killing pines in many areas of central and eastern Iowa, especially those planted on golf courses and other areas for ornamental purposes. Most reports concern Austrian Pine (*Pinus nigra* Arnold).

LONGIDORIDAE (Thorne, 1935) Meyl, 1961

Longidorus (Micoletzky, 1922) Meyl, 1961 generally contain the largest plant-parasitic nematodes known, some becoming 6-8 mm in length. Numbers are usually few, except with one species associated with corn.

L. breviannulatus Norton & Hoffmann, 1975 is one of the most damaging nematodes in maize in highly sandy soils (30). It causes root pruning of seedlings resulting in severe stunting and greatly reduced yields. The nematode has been found in most sandy fields examined in the central and southwestern counties of the state where maize has been grown continuously for a few years.

L. crassus Thorne, 1974. This species was reported to occur around roots of *Quercus alba* near Ames (55).

L. macromucronatus Siddiqi, 1962 was associated with *Acer saccharinum* and *Carya ovata* at the Childs Access in Black Hawk County, and was also found along the Des Moines River near Madrid.

L. sylphus Thorne, 1939 (?) was found only around *Ostrya virginiana* at Hanging Bog in Linn County. This species originally reported as *L. sylphus* (37) in Iowa is now thought to be a new species (R. Robbins, University of Arkansas, personal communication).

Xiphinema Cobb, 1913.

X. americanum Cobb, 1913 is one of the most common of the plant-parasitic nematodes in cultivated fields, and is also one of the most serious pathogens. Although in Iowa, pathogenicity has been demonstrated only with maize and alfalfa, the species probably causes damage to many crops. The nematode is also common in prairies, but rare in woodlands.

X. bakeri Williams, 1961. This large species was found only four times. It was associated with *Acer saccharum* in the Retz Memorial, *Carya ovata* and *Adiantum pedatum* L. in the Yellow River State Forest, and *Tilia americana* at Maquoketa State Park. Numbers were few.

X. chambersi Thorne, 1939. This species was found 28 times, usually in small numbers and mainly in mesic woodlands. The most found were 50 around *Quercus rubra* in Heery Woods State Park and around *Carya ovata* south of New Albin. The nematode was found twice in maize fields adjacent to woods. The mean for all samples was 18. The nematode also occurs in wetter sites in Iowa prairies (45).

X. rivesi Dalmasso, 1969. This is almost strictly a woodland species and was found around 42 of the 47 plant species sampled in this habitat. The nematode was found in 212 of 358 samples from woodlands for a frequency of 59%. It was found in 80% of the 40 samples around *Acer saccharum*. The nematode was not found in 15 *Abies balsamea* samples. It was recovered only twice outside woodlands. The greatest number was 760 around *Juglans nigra* in Idlewild Park, Floyd County. Considering the relatively large size of the nematode, the numbers obtained were many. The average number per sample was 80. The greatest numbers were recovered in the more mesic areas of woodlands, possibly a reflection of the host habitat as well as the nematode. Mean numbers around conifers were generally much fewer than around broadleaf trees.

TRICHODORIDAE (Thorne, 1935) Clark, 1961

Trichodorus Cobb, 1913 and *Paratrichodorus* (Colbran, 1956) Siddiqi, 1974.

T. proximus Allen, 1957 is mainly a prairie inhabitant found at the Freda Haffner Kettlehole and at the Cayler, Kalsow, and Cedar Hills Sand prairies. Numbers were under 60 per sample.

P. minor is known best in maize fields in highly sandy soils where it is sporadic in occurrence.

ECOLOGICAL NOTES ON THE OCCURRENCE OF PLANT-PARASITIC NEMATODES IN IOWA

Frequency Distributions.

A typical frequency distribution for nematodes is illustrated by *H. platyurus* in woodlands in Fig. 1. Most samples in which a given species is found contain relatively few individuals, with few samples containing many individuals of the nematode in question.

Occurrences of Nematodes by Associated Trees

As in most local biota distributions, a few species often are abundant to common with the remaining being infrequent of rare. As an example, of the species identified in the Iowa woodlands the eight (*Xiphinema rivesi* > *Helicotylenchus platyurus* > *Criconemella macrodora* > *Ogma octangulare* > *Criconemella xenoplax* > *Ogma menzeli* > *Gracilacus straeleni* > *Criconemella incrassata*) most common in percentage of times found comprised 79% of all the plant-parasitic nematodes recovered in this habitat. The most numerous, however may not be the most important biologically as based on fresh weight as calculated by Andrassy's method (2). The third most numerous species in woodlands (*X. rivesi*) had over six times the biomass of the most numerous species (*C. macrodora*).

Occurrences of four common nematodes associated with the seven trees sampled most commonly in woodlands is depicted in Table 2. *X. rivesi* was associated most frequently and was most numerous around *A. saccharum* and least around *P. strobus*. The mean number of *O. menzeli* was greatest around *Q. alba* but was not found around *P. strobus*. Although *C. macrodora* was not as frequent as *H. platyurus* and *X. rivesi* it was generally the most numerous and is a reflection of its small size compared with the others. Although *O. menzeli* is about the same size as *C. macrodora*, the differences in occurrences and numbers indicate differences in possible degrees of parasitism. Because associations do not prove parasitism, controlled studies are needed to provide more definite answers.

Sorensen's Similarity Indices

Even though sampled the most, fields of maize contained the fewest species, 27 for maize compared with 43 species in prairies, and 44 species in woodlands. The greatest degree of similarity was in the maize-prairie ecosytems (0.49) and the least in the maize-woodland ecosystems (0.23). The prairie woodlands index was 0.37. Because maize is a grass and prairies contain many grasses, it seems logical to conclude that nematodes would have affinities for similar types of vegetation even though maize is an annual and most prairie grasses are perennials. Such similarities are only general, however. Species of *Pratylenchus* are rare in prairies and woodlands but are among the most common nematodes in corn and soybean fields. Agriculture undoubtedly has favored species of this genus.

Diversity and Evenness

Diversity (H') of species in prairies, woodlands, and maize habitats were 2.74, 1.65, and 1.07, respectively. Eveness (J') of species in the three habitats were 0.78, 0.48, and 0.41, respectively. Thus, H's and J's were highest in the prairies and lowest around maize. The monoculture of maize and the diveristy of plants in prairies probably account for these differences even though both are basically grass habitats. The higher H' in prairies than in woodlands agrees with studies in Montana (58), Poland (57), Switzerland (8), and New Zealand (10) where either numbers of diversities of nematode species or genera were greatest in grasslands and least in forests or cultivated areas.

This report brings up to date the known distributions of plant-parasitic nematodes in Iowa. Of the 99 species of nematodes reported here, 27 are new state records. There is no illusion that this report is definitive. Most knowledge on plant and soil nematodes in Iowa

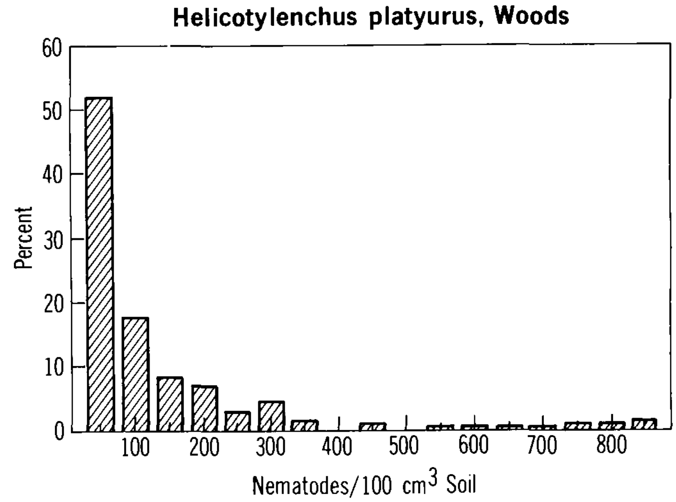

Fig. 1. Frequency distribution of *Helicotylenchus platyurus* in Iowa woodlands.

Table 2. Occurrences of four common nematodes associated with the most frequently sampled tree species in Iowa woodlands. 1984-1987.

Associated plant[1]	Nematode			
	Helicotylenchus platyurus[2]	*Criconemella macrodora*[2]	*Ogma menzeli*[2]	*Xiphinema rivesi*[2]
Acer saccharum (40)	50-125-840	23-226-1,400	28-49-330	80-100-540
Ostrya virginiana (38)	63-59-220	37-312-3,000	26-24-100	58-69-370
Quercus rubra (21)	57-103-260	48-215-1,400	38-87-300	52-65-380
Pinus strobus (19)	42-64-280	21-453-800	0-0-0	32-19-260
Carya ovata (18)	72-54-190	39-236-1,300	44-21-40	44-77-300
Quercus alba (18)	61-112-770	61-150-825	22-116-288	61-31-70
Tilia americana (18)	44-18-40	22-76-200	33-58-190	39-61-140

[1]Numbers in ( ) are the times the species was sampled.

[2]The first number is the frequency of recovery around the tree sampled, the second is the average number of individual numbers recovered, and the third is the maximum number in any sample. Numbers are per 100 cm^3 soil.

remains to be discovered. The economic impact on plants for most nematode species, as well as their interrelationships with other biota, is largely unknown.

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REFERENCES

1. ALLEN, M.W. 1955. A review of the nematode genus *Tylenchorhynchus*. Univ. Calif. Publ. Zool. 61:129-166.
2. ANDRÁSSY, I. 1956. The determination of volume and weight of nematodes. Acta Zoologica. (Hungarian Acad. Sci. 2(1-3):1-15 *in* B.M. Zuckerman, M.W. Brzeski, and K.H. Deubert (Eds.). English translation of selected East European papers in nematology. University of Massachusetts. 1967.
3. BALDWIN, J.G., and A.H. BELL. 1981. *Pararotylenchus* n. gen. (Pararotylenchinae n. subfam., Hoplolaimidae) with six new species and two new combinations. J. Nematol. 13:111-128.
4. BIRD, G.W. 1971. Influence of incubation solution on the rate of recovery of *Pratylenchus brachyurus* from cotton roots. J. Nematol. 3:378-385.
5. BOAG, B., and M.S. JAIRAJPURI. 1985. *Helicotylenchus scoticus* n. sp. and a conspectus of the genus *Helicotylenchus* Steiner, 1945 (Tylenchida: Nematoda). Syst. Parasitol. 7:47-58.
6. BRZESKI, M.W. 1974. Taxonomy of Hemicycliophorinae (Nematoda, Tylenchida). Zesz. Probl. Postepow Nauk Roln. 154:237-330.
7. BRZESKI, M.W. 1977. Nicienie pasozyty roslin. Podrzad Tylenchina. Warsaw, Poland; Panstwowe Wydawnictwo Naukowe. 87 pp.
8. BURKHALTER, M. 1928. Die Verbreitung der freilebenden Erdnematoden in verschiedenen Gelandarten in Massif der Rochers de Naya (2045 m.). Rev. Suisse Zool. 35:389-437.
9. DONALD, P.A., and R.M. HOSFORD, JR. 1980. Plant parasitic nematodes of North Dakota. Plant Dis. 64:45-47.
10. EGUNJOBI, O.A. 1971. Soil and litter nematodes of some New Zealand forests and pastures, N.Z. J. Sci. 14:568-579.
11. FORTUNER, R. 1987. A reappraisal of Tylenchina (Nemata). 8. The family Hoplolaimidae Filip'ev, 1934. Rev. Nématol. 10:219-232.
12. FORTUNER, R., and A.R. MAGGENTI. 1987. A reappraisal of Tylenchina (Nemata). 4. The family Anguinidae Nicoll, 1935 (1926). Rev. Nématol. 10:163-176.
13. FORTUNER, R., and M. LUC. 1987. A reappraisal of Tylenchina (Nemata). 6. The family Belonolaimidae (Whitehead, 1960). Rev. Nématol. 10:183-202.
14. FORTUNER, R., A.R. MAGGENTI, and L. WHITTAKER. 1984. Morphometrical variability in *Helicotylenchus* Steiner, 1945. 4: Study of field populations of *H. pseudorobustus* and related species. Rev. Nématol. 7:121-135.
15. FORTUNER, R., G. MERNY, and C. ROUX. 1981. Morphometrical variability in *Helicotylenchus* Steiner, 1945. 3: Observations on African populations of *Helicotylenchus dihystera* and considerations on related species. Rev. Nématol. 4:235-260.
16. GOLDEN, A.M., and D.J. RASKI. 1977. *Heterodera thornei* n. sp. (Nematoda: Heteroderidae) and a review of related species. J. Nematol. 9:93-112.
17. HOFFMANN, J.K. 1974a. *Discocriconemella inaratus* n. sp. and *Criconemoides inusitatus* n. sp. (Nematoda) from Iowa. J. Nematol. 6:210-214.
18. HOFFMANN, J.K. 1974b. Morphological variation in species of *Bakernema*, *Criconema*, and *Criconemoides* (Criconematidae: Nematoda). Iowa State J. Res. 49:137-153.
19. HOFFMANN, J.K., and D.C. NORTON. 1976. Distribution patterns of some Criconematinae in different forest associations. J. Nematol. 8:32-35.
20. HOPPER, B.E. 1959. Three new species of the genus *Tylenchorhynchus* (Nematoda: Tylenchida). Nematologica 4:23-30.
21. JENKINS, W.R. 1964. A rapid centrifugal-flotation technique for separating nematodes from soil. Plant Dis. Rep. 48:692.
22. KERR, E.D., and D.S. WYSONG. 1979. Sting nematode. *Belonolaimus* sp., in Nebraska. Plant Dis. Rep. 63:506-507.
23. KNOBLOCH, N.A. 1971. Emendation of the description of *Tylenchorhynchus longus* Wu, 1969. Nematologica 17:602-603.
24. LOOF, P.A.A. 1978. The genus *Pratylenchus* Filipjev, 1936 (Nematoda: Pratylenchidae): A review of its anatomy, morphology, distribution, systematics and identification. Swedish Univ. Agric. Sci. Res. Infor. Cent. Uppsala. 50 pp.
25. LUC, M. 1987. A reappraisal of Tylenchina (Nemata). 7. The family Pratylenchidae Thorne, 1949. Rev. Nématol. 10:203-218.
26. LUC, M., and R. FORTUNER. 1987. A reappraisal of Tylenchina (Nemata). 5. The family Dolichodoridae Chitwood, 1950. Rev. Nématol. 10:177-181.
27. LUC, M., and D.J. RASKI. 1981. Status of the genera *Macroposthonia*, *Criconemoides*, *Criconemella* and *Xenocriconemella* (Criconematidae: Nematoda). Rev. Nématol. 4:3-21.
28. LUC, M., A.R. MAGGENTI, and R. FORTUNER. 1988. A reappraisal of Tylenchina (Nemata). 9. The family Heteroderidae Filip'ev & Schuurmans Stekhoven, 1941. Rev. Nématol. 11:159-176.
29. MAGGENTI, A.R., M. LUC, D.J. RASKI, R. FORTUNER, and E. GERAERT. 1987. A reappraisal of Tylenchina (Nemata). 2. Classification of the suborder Tylenchina (Nemata: Diplogasteria). Rev. Nématol. 10:135-142.
30. MALEK, R.B., D.C. NORTON, B.J. JACOBSEN, and N. ACOSTA. 1980. A new corn disease caused by *Longidorus breviannulatus* in the Midwest. Plant Dis. 64:1110-1113.
31. NORTON, D.C. 1983. Occurrence and distribution of plant-parasitic nematodes associated with maize in Iowa. Proc. Iowa Acad. Sci. 90:88-92.
32. NORTON, D.C, and J.K. HOFFMANN. 1974. Distribution of selected plant-parasitic nematodes relative to vegetation and edaphic factors. J. Nematol. 6:81-86.
33. NORTON, D.C., and M. OARD. 1981. Plant-parasitic nematodes in loess toposequences planted with corn. J. Nematol. 13:314-321.
34. NORTON, D.C., and D.P. SCHMITT. 1978. Community analyses of plant-parasitic nematodes in the Kalsow Prairie, Iowa. J. Nematol. 10:171-176.
35. NORTON, D.C., and F. VARON de AGUDELO. 1984. Plant-Gparasitic nematodes associated with maize in Cauca and Valle del Cauca, Colombia. Plant Dis. 68:950-952.
36. NORTON, D.C., A.M. CODY, and A.W. GABEL. 1987. *Subanguina calamagrostis* and its biology in *Calamagrostis* spp. in Iowa, Ohio, and Wisconsin. J. Nematol. 19:260-262.
37. NORTON, D.C., D. DUNLAP, and D.D. WILLIAMS. 1982. Plant-parasitic nematodes in Iowa: Longidoridae and Trichodoridae. Proc. Iowa Acad. Sci. 89:15-19.
38. PIELOU, E.C. 1975. Ecological diversity. New York. Wiley-Interscience. 165 pp.
39. RASKI, D.J., and M. LUC. 1984. A reappraisal of the genus *Criconema* Hofmanner & Menzel, 1914 (Nematoda: Criconematidae). Rev. Nématol. 7:323-334.
40. RASKI, D.J., and M. LUC. 1987. A reappraisal of Tylenchina (Nemata) 10. The superfamily Criconematoidea Taylor, 1936. Rev. Nématol. 10:409-444.
41. RAU, G.J. 1963. Three new species of *Belonolaimus* (Nematoda: Tylenchida) with additional data on *B. longicaudatus* and *B. gracilis*. Proc. Helminthol. Soc. Wash. 30:119-128.
42. RIGGS, R.D., H. HIRSCHMANN, and M.L. HAMBLEN. 1969. Life cycle, host range, and reproduction of *Heterodera betulae*. J. Nematol. 1:180-183.
43. SCHMITT, D.P. 1973a. Population fluctuations of some plant parasitic

nematodes in the Kalsow Prairie, Iowa. Proc. Iowa Acad. Sci. 80:69-71.
44. SCHMITT, D.P. 1973b. Soil property influences on *Xiphinema americanum* populations as related to maturity of loess-derived soils. J. Nematol. 5:234-240.
45. SCHMITT, D.P., and D.C. NORTON. 1972. Relationships of plant parasitic nematodes to sites in native Iowa prairies. J. Nematol. 4:200-206.
46. SEINHORST, J.W. 1959. Two new species of *Pratylenchus*. Nematologica 4:83-86.
47. SEINHORST, J.W. 1968. Three new *Pratylenchus* species with a discussion of the structure of the cephalic framework and of the spermatheca in this genus. Nematologica 14:497-510.
48. SIDDIQI, M.R. 1986. Tylenchida, Parasites of Plants and Insects. Commonwealth Inst. Parasitol. Farnham Royal Slough SL2 3BN England.
49. SMOLIK, J.D. 1977. Nematodes associated with irrigated corn in South Dakota. Proc. S.D. Acad. Sci. 56:93-99.
50. SMOLIK, J.D., and R.B. MALEK. 1972. *Tylenchorhynchus nudus* and other nematodes associated with Kentucky bluegrass turf in South Dakota. Plant Dis. Pre. 56:898-900.
51. SORENSEN, T. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content and its application to analyses of the vegetation on Danish Commons. K. Danske Biol. Skr. Copenhagen 5(4):1-34.
52. STURHAN, D. 1981. Studies on *Geocenamus* species from Germany (Nematoda, Dolichodoridae). Nematologica 27:306-314.
53. SZCZYGIEL, A. 1970. *Tylenchorhynchus polonicus* sp. n. and *Helicotylenchus pseudodigonicus* sp. n. (Nematoda, Tylenchoidea) from Poland. Bull. l'Acad. Pol. Sci. Ser. Sci. Biol. Cl.V. 17:685-690.
54. THOMAS, S.H., and D.C. NORTON. 1986. Influence of selected maize hybrids on nematode populations under differing edaphic conditions. Plant Dis. 70:234-237
55. THORNE, G. 1974. Nematodes of the Northern Great Plains. Part II. DORYLAIMOIDEA in part (NEMATA: ADENOPHOREA). S.D. Agric. Exp. Stn. Tech. Bull. 41. 120 pp.
56. THORNE, G., and R.B. MALEK. 1968. Nematodes of the Northern Great Plains. S.D. Agric. Exp. Stn. Tech. Bull. 31. 111 pp.
57. WASILEWSKA, L. 1979. The structure and function of soil nematode communities in natural and agrocenoses. Polish Ecol. Stud. 5:(2)97-146.
58. WEAVER, T., and J. SMOLIK. 1987. Soil nematodes of northern Rocky Mountain ecosystems: genera and biomasses. Great Basin Nat. 47:473-479.
59. WILLIAMS, D.D. 1982. The known Pratylenchidae (Nematoda) of Iowa. Iowa State J. Res. 56:419-424.
60. WU, L-Y. 1965. Five new species of *Criconemoides* Taylor, 1936 (Criconematidae: Nematode) from Canada. Can. J. Zool. 43:203-214.
61. WU, L-Y. 1967. *Anguina calamagrostis*, a new species from grass, with an emendation of the generic characters for the genera *Anguina* Scopoli, 1777 and *Ditylenchus* Filipjev, 1936 (Tylenchidae: Nematode). Can. J. Zool. 45:1003-1010.
62. WU, L-Y. 1969. Three new species of the genus *Tylenchorhynchus* Cobb, 1913 (Tylenchidae: Nematoda) from Canada. Can. J. Zool. 47:563-567.